

# Salient features in locomotor evolutionary adaptations of proboscideans revealed via the differential scaling of limb long bones

By Valery B. Kokshenev and Per Christiansen

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**Abstract.** The standard differential scaling of proportions in limb long bones (length against circumference) is applied to a phylogenetically wide sample of the Proboscidea, Elephantidae and the Asian (*Elephas maximus*) and African elephant (*Loxodonta africana*). In order to investigate allometric patterns in proboscideans and terrestrial mammals with parasagittal limb kinematics, the computed slopes (slenderness exponents) are compared with published values for mammals and studied within a framework of theoretical models of long bone scaling under gravity and muscle forces. Limb bone allometry in *E. maximus* and the Elephantidae are congruent with adaptation to bending and/or torsion induced by muscular forces during fast locomotion, as in other mammals, whereas limb bones in *L. africana* appear adapted for coping with the compressive forces of gravity. Consequently, hindlimb bones are expected to be more compliant than forelimb bones in accordance with in vivo studies on elephant locomotory kinetics and kinematics, and the resultant negative limb compliance gradient in extinct and extant elephants, which contrasts to other mammals, suggests an important locomotory constraint preventing achievement of a full-body aerial phase during locomotion. Differences in ecology may be responsible for the subtle differences observed between African and Asian elephant locomotion, and the more pronounced differences in allometric and mechanical patterns established in this study.

*Key words:* long bone scaling models; standard differential scaling; limb gradient functions; proboscideans; extinct and extant elephants.

## I. INTRODUCTION

Differential scaling of the proportions of the limb long bones in terrestrial mammals has been studied by many researchers (most often bone length  $L$  and circumference  $C$  or diameter

$D$ ) with the aim to establish correlations between design and posture of mammalian limbs coping with support of mass and locomotion in the gravitational field. Many attempts to formulate generally applicable allometric power laws ( $L \propto M^l$  and  $C = \pi D \propto M^d$ , where  $M$  is body mass) have been the subject of a long standing debate and controversy (e.g., McMahon 1973, 1975a, b; Alexander 1977; Alexander et al. 1979a; Biewener 1983, 2005; Economos 1983; Bertram & Biewener 1990; Christiansen 1999a, b, 2002, 2007; Kokshenev, 2003, 2007; Kokshenev et al. 2003). Among the proposed theoretical frameworks, the three most common of which are: the *geometric* (or isometric) *similarity model* (GSM, with  $l_0 = d_0 = 1/3$ ); the *elastic similarity model* (ESM, with  $l_0 = 1/4, d_0 = 3/8$ ); and the static *stress similarity model* (SSM, with  $l_0 = 1/5, d_0 = 2/5$ ). Subsequently, these similarity models have typically been explored in analysis of allometric power laws using measured bone lengths and diameters resulted in allometric exponents ( $l$  and  $d$ ), when body masses are available. In cases where body masses are unknown, a *slenderness exponent*  $\lambda$  can be computed (via  $L \propto C^\lambda$ ) and compared with that predicted as  $\lambda_0 = l_0/d_0 = 1, 2/3$ , or  $1/2$  by the GSM, ESM, and SSM, respectively (McMahon 1975a).

Originally proposed to explain animal design to experience similar elastic forces and stresses under gravity, the corresponding ESM (or "buckling" model) and SSM (McMahon 1973, 1975a, b) were found not to apply to terrestrial mammals as a group, neither overall body proportions (Economos 1983; Silva 1998), nor allometric scaling of long bones (Alexander et al. 1979a; Biewener 1983, 2005; Economos 1983; Christiansen 1999a, b; Kokshenev et al. 2003). Instead, body proportions and long bones were found closer to isometry, i.e., to GSM with  $\lambda_0 = 1$ , and in large mammals and in large mammals they both become progressively more robust with increments in body size. Testing McMahon's models, many studies indicated that muscle forces, showing size-dependent fluctuations among terrestrial mammals, are highly important (e.g., Alexander 1985, Biewener 1983, 1989, 1990, 2005). Direct evidences of muscle forces affecting proportions of the allometric scaling of the major long bones in Artiodactyla were provided by Selker and Carter (1989). It was analytically shown that the failure of any one predicted power law was shown not caused by the failure of underlying elastic force patterns but due to McMahon's simplifications for evolutionary adaptive properties for maintaining similar skeletal functional stresses apart of muscles and under the dominating influence of gravity (Kokshenev et al. 2003). Then, using the overall-bone slenderness exponent  $\lambda_{\text{exp}}^{(\text{mam})} = 0.80 \pm 0.02$ , resulting from re-analysis of bone proportions in

a wide-ranging sample of terrestrial mammals from Christiansen (1999a), also not matching any of McMahon's original predictions, the dominating role of muscle forces in long-bone scaling was demonstrated from first physical principles (Kokshenev 2003).

Naturally, bone shape is a hereditary property, but bone is a phenotypically plastic tissue, capable of reacting powerfully to its mechanical environment. In the growing fetus, bone shape, size and position is initially determined by the early cartilaginous anlagen during embryonic skeletogenesis, which are subsequently gradually replaced by endochondral ossification during ontogeny (Favier & Dollé 1997; Currey 2003; Provet & Schipani 2005). However, bone shape is heavily influenced by a mechanical response to the environment during ontogeny and throughout an animal's life. It has been demonstrated that strain rate and magnitude, surrounding tissue formation, and fetal muscle contractions are prerequisites for normal bone formation during ontogeny (Rodriguez et al. 1992; Mosley et al. 1997; Mosley & Lanyon 1998; Lamb et al. 2003). In post-natal and adult mammals, bone is capable of reacting to changes in mechanical stresses enforced by physical activity and muscle mechanics with rapid alterations of size and shape (Biewener 1983, 1989, 1990; Carrano & Biewener 1999; Curry 2003; Firth et al. 2005; Warden et al. 2005; Franklyn et al. 2008), and hereditary properties determined by the genome appear primarily responsible for bone patterning during fetal ontogeny and is less relevant for bone size and shape in the adult animal (Mariani & Martin 2003). These factors are seemingly beyond macroscopic elastic theories for formulating allometric power laws for bone scaling. Moreover, the concept of uniform elastic similarity also seems to be inconsistent with a diversity of functional local elastic forces and stresses, which are not constant in bones during locomotion and therefore are not likely to be reflected in scaling analysis of external bone dimensions (Doube et al. 2009). Nevertheless, the authors hopefully believe that scaling predictions arising from the macroscopic spatial continuous mechanics applied to bone tissue under broad spectrum of loading conditions (Kokshenev et al. 2003), and therefore reflecting most general trends in proportional limb bone adaptations to environmental conditions, can be reliably verified at least by the overall limb and bone allometric data.

The above bone scaling studies and other statistical and experimental studies (e.g., Biewener et al. 1983a, b, 1989; Rubin & Lanyon 1984; Selker & Carter, 1989; Streicher & Muller 1992; Carrano & Biewener 1999) have stimulated formulation of novel theoretical concepts in light of dynamic bone strain similarity (Rubin & Lanyon, 1984) or mechanical

(strain and stress) similarity (Kokshenev 2007). Basic conceptions of McMahon's (1973, 1975a) elastic similarity hypothesis have also been reconsidered (Kokshenev et. al., 2003, Kokshenev 2003). The framework of bone scaling is, by default, limited to long bones approximated by cylinders with  $L \gg D$  justified by the ratio  $L/D \sim 10$ , at least for mammalian humerus, radius, ulna, femur, and tibia. Moreover, the justification for application of the elastic theory patterns established for arbitrary loaded long solid cylinders (Kokshenev 2007) is generally based on the assumption that the long bones play the primary role in body support. Consequently, the positive allometry of long bone structure in relation to body mass observed in regression analysis may be expected to be better understood by biomechanical adaptation of bones to maximal external loads emerging during fast locomotion and studied via bone-reaction elastic forces and stresses, whereas non-mechanical ontogeny effects of limb bone adaptation associated with a small Prange's index are relatively small (Kokshenev 2007).

In the present study we analyze the surprisingly varied differential scaling of the limb long bones in a taxonomically narrow clade of mammals, the extant proboscideans (Proboscidea, Elephantidae); the Asian elephant (*Elephas maximus*), and African savannah elephant (*Loxodonta africana*). These gigantic land mammals have a more upright limb posture, notably much more upright propodials and different locomotor mechanics from other terrestrial mammals in that fast locomotion is ambling with no suspended phase in the stride, but with duty factors  $\beta > 0.5$  (Gambaryan 1974; Alexander et al. 1979b; Hutchinson et al. 2003, 2006). We compare theoretical predictions with the data from a phylogenetically wide sample of extinct proboscideans from Christiansen (2007) completed here by the Elephantidae family, as well as allometry results from scaling studies of running mammals with parasagittal limb kinematics, in the hope of establishing generic allometric patterns distinguishing limb postures characteristic of high-power locomotion in proboscideans and mammals.

Modern elephants are characteristic in having very long limb bones for their body size (Christiansen 2002), and a very upright, though not strictly columnar (Ren et al. 2007), limb posture, in which the two propodial bones (femur and in particular humerus) are kept at a distinctly greater angle compared to the ground than is the case in other large, quadrupedal mammals. The steeply inclined propodials imply that during standing and at low speeds, the primary forces affecting the limb bones will be axially compressive. However, with increments in speeds, joint flexion increases during the support phase, and during the

recovery phase, joint flexion can be high (Ren et al. 2007). Although there is no difference in joint flexion between juvenile and adults or between Asian and African elephants, the propodial bones are still markedly more inclined compared to horizontal even during the fast locomotion than is in the case for other quadrupedal running mammals. During the support phase in locomotion, the ankle, unlike the more mobile wrist, displays spring-like mechanical properties, reminiscent of, albeit less than in quadrupedal running mammals, matching the more compliant hind limbs during locomotion. This also is consistent with the tendons of the hind-foot scaling with positive allometry during ontogeny, whereas those of the forelimb scale with negative allometry, and thus become progressively more gracile (Miller et al. 2008), thereby supporting the observation that the hindlimbs are more compliant with bouncing kinematics than the stiffer, vaulting forelimbs, during fast locomotion. In view of the progress in application of bone scaling models (Kokshenev 2003, 2007), a general problem arises whether kinematic evidences on the mechanical influence on bone ontogeny can be independently revealed by the differential limb bone scaling?

## II. MATERIALS AND METHODS

### A. Theoretical background

A theoretical analysis of non-critical elastic forces emerging in long bones of adult mammals resulted in mode-independent relationships for bone scaling exponents

$$d = \frac{1}{3} + b \text{ and } l = \frac{1}{3} - b, \text{ with } \lambda(b) = \frac{l}{d} = \frac{1 - 3b}{1 + 3b} \quad (1)$$

discussed in Eq. (8) in Kokshenev 2007. Here  $b$  is Prange's index scaling bone mass to body mass. Since scaling index  $b$  is consistently small for mammals (see e.g. table 1 in Kokshenev 2003), equation (1) matches previous observations mentioned in Introduction of the closeness of mammalian bone allometry to isometry. Accordingly, small deviations from the force-isotopic GSM are described via the directly observable model-independent index  $b$ . The differential scaling data for mammals (Christiansen 1999a, 1999b) supports the physically justified inequalities  $d > 1/3 > l$  (Kokshenev 2007) providing the constraint  $\lambda(b) < 1$ , resulting in  $b < 1/6$  following from equation (1). The empirically established constraint  $b_{\text{exp}}^{(\text{mam})} = 0.04 \pm 0.01$ , for overall-averaged long bones in mammalian limbs (see

table 1 in Kokshenev 2007), results in the *model-independent* pattern, namely

$$d_{pre}^{(mam)} = 0.37 \pm 0.01 \text{ and } l_{pre}^{(mam)} = 0.29 \pm 0.01, \text{ or } \lambda_{pre}^{(mam)} = 0.785 \pm 0.025 \quad (2)$$

predicted for mammals capable of true running with a fully suspended aerial phase in the stride [1].

As for McMahon's models discussed in Introduction and revised by Kokshenev (2003, 2007) and Kokshenev et al. (2003), they can be broadly interpreted as follows. If both gravitational and muscular competitive forces driven by structural bone adaptation to complex (axial and non-axial) compression were equally important in bone interspecific allometry, the observed statistically overall-bone slenderness exponent  $\lambda_{exp}$  is expected to be nearly isometric, i.e., close to maximum  $\lambda_0 = 1$ , following from the GSM. If, however, gravitational forces were dominating, bone proportions could be expected to become optimized for exploitation of long bone stiffness during modes of fast locomotion in mammals with near parasagittal limb kinematics, and would result in  $\lambda_0 = 2/3$ , as predicted by the ESM, as predicted by the ESM, also known as the buckling model. Although the ESM was originally introduced for the states of elastic instability (McMahon 1973) or thermodynamic instability (Kokshenev et al. 2003), the domain of resulting scaling relations extends far below critical amplitudes of forces (and critical stresses and strains), which should still exclude non-axial elastic forces (Kokshenev 2007). In contrast, the adaptation to faster forms of locomotion via more compliant long bones subjected to the non-axial compression could be observed via the exponent  $\lambda_0 = 1/2$ , predicted by the SSM, treated as a "bending-torsion" model (Kokshenev 2007). As an example of theoretical rationalization underlying these two distinct patterns of bipedal locomotion in the sagittal plane, a transition from stiff-limbged slow-walking to the compliant-limbged fast walking following by running was illuminated in terms of a dynamic instability of the trajectory of center of gravity in humans (Kokshenev 2004).

When muscle forces play a dominating role in the formation of bone proportions, the appropriate modified model for bone evolution (hereafter termed SSMM) predicts  $\lambda_{pre}^{(bend)} =$

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[1] It seems to be interesting to compare the proposed empirical exponent  $\lambda_{mod}^{(mam)} = 0.785$ , substituting McMahon's  $\lambda_0 = 1/2$ , with the theoretical estimate  $\lambda_{mod} = 7/9 (\approx 0.778)$  obtained on the basis of a pattern of non-axial elastic forces in bone resisting functionally relevant limb muscles (Kokshenev 2008). The bone-muscle scaling theory will be discussed elsewhere.

$0.80 \pm 0.03$ , as derived from both allometric mammalian limb bone and muscle data (see equation (18) in Kokshenev 2003). Since this prediction is congruent with the one made in equation (2), we infer that mammalian long bones are designed to resist peak bending and/or torsional bone compressions produced by muscles during fast running modes, that was initially established via bending functional bone stress (Rubin & Lanyon 1982) and then explained analytically (see figure 1 in Kokshenev 2007). For mammals as group, we therefore use the SSMM estimate  $\lambda_{\text{mod}}^{(\text{mam})} = 0.785$  predicted semi-empirically in equation (2) and theoretically in [1].

## B. Materials and analysis

We used previously published data on external limb long bone dimensions from 19 species and 217 specimens of proboscideans (Christiansen 2007), which was supplemented by new data collected for the purpose of this study. We compared this to published data from 79 and 98 species of running mammals from Christiansen 1999a and 1999b, respectively. We conducted regression analysis on  $\text{Log}_{10}$  transformed external limb long bone articular lengths and diaphysial diameters using the standard *least squares* (LS) and *reduced major axis* (RMA) methods. All species with multiple specimens were averaged prior to analysis. The significances of the regression parameters were evaluated by computing the correlation coefficient, the standard error of the estimate, and the F-statistic of the regressions, and the 95% confidence intervals for the regression intercepts and slopes (see online electronic supplementary material). The regression analysis included the entire Proboscidea; the Elephantidae (*Elephas* sp., *Loxodonta africana*, and *Mammuthus* sp.). We computed separate regression analyses for the extant Asian elephant (*Elephas maximus*) and African savannah elephant (*Loxodonta africana*), since these are, by default, the only taxa for which locomotory information exists; we included no data from the forest elephant (*Loxodonta cyclotis*) within the African elephant, because this taxon most likely constitutes a separate species (Barriel et al. 1999).

### III. RESULTS

Searching for generic morphometric patterns in long bones via external dimensions, to which the similarity models (McMahon 1973, 1975a; Kokshenev 2003, 2007; Kokshenev et al. 2003) are broadly addressed, we study the slenderness bone exponent  $\lambda$  as directly observed by the slopes in plots  $\text{Log}_{10}L$  vs  $\text{Log}_{10}C$ . In table 1, the results of bone-size regression analysis in species-averaged specimens of proboscideans are compared with those for mammals.

Species	Elephantidae			Proboscidea			Mammals		
Limb bones	<i>N</i>	$\lambda$	<i>r</i>	<i>N</i>	$\lambda$	<i>r</i>	<i>N</i>	$\lambda$	<i>r</i>
Humerus	7	0.912	0.990	16	<i>1.134</i>	0.831	189	0.7631	0.9738
Radius	6	0.813	0.853	10	<i>1.078</i>	0.878	189	0.7530	0.9957
Ulna	6	0.727	0.888	14	0.929	0.866	189	0.849*	0.9600
Femur	7	0.747	0.966	14	0.802	0.816	189	0.8431	0.9763
Tibia	6	0.751	0.925	11	0.772	0.857	188	0.7641	0.9499
Limb bone, LS	6	<b>0.790</b>	0.924	13	<b>0.943</b>	0.850	189	<b>0.795</b>	0.971
Limb bone, RMA	6	<b>0.856</b>	0.924	13	<b>1.165</b>	0.850	189	<b>0.778</b>	0.971

**Table 1.** The statistical data on the slenderness of individual and effective limb bones in animals. The data for Elephantidae and Proboscidea are shown on the basis of regression data provided in online electronic supplementary material, extending table 2 in Christiansen 2007, and these for mammals are taken from table 2 in Christiansen 1999b. The mean *slenderness exponents*  $\lambda = d\text{Log}_{10}L/d\text{Log}_{10}C$  presented by the slopes ( $\lambda$ ) exemplified in figure 1 are observed in *N species* through the LS regression of with the *correlation coefficient r*. The limb bone LS characterization corresponding to the overall-bone mean data is introduced by the standard mean over all 5 bones. The RMA data in the last row are shown only for the resulting limb bone data. The bold numbers are the data used below in figures. The italic numbers indicate the slope data contrasting to mammalian data with  $\lambda < 1$  (see also discussion in section 2.1 in the Methods). \*) The data estimated with the help of ratio  $l/d$  for the ulna allometric exponents taken from table 2 in Christiansen 1999a.

In figure 1 and table 2, we analyze modern elephants.

## Place figure 1

Species	<i>E. maximus</i>			<i>Loxodonta africana</i>				
	<i>n</i>	$\lambda$	<i>r</i>	<i>n</i>	$\lambda$	<i>r</i>	$p_{min}$	$p_{max}$
Limb bones								
Humerus	22	0.754	0.985	14	0.616	0.978	0.01	0.02
Radius	19	1.014	0.987	8	0.675	0.994	—	0.001
Ulna	20	0.818	0.981	11	0.644	0.979	0.01	0.02
Femur	25	0.758	0.972	13	0.618	0.986	0.01	0.02
Tibia	20	0.913	0.970	10	0.688	0.939	0.02	0.05
Forelimb bone	20	0.862	0.984	11	0.645	0.984	0.01	0.02
Hindlimb bone	23	0.836	0.971	12	0.653	0.963	0.015	0.035
Limb bone, LS	21	<b>0.851</b>	0.979	11	<b>0.648</b>	0.975	0.013	0.028
Limb bone, RMA	21	<b>0.869</b>	0.979	11	<b>0.665</b>	0.975	0.013	0.028

**Table 2.** The statistical data on  $\log_{10}L$  vs  $\log_{10}C$  regression for individual limb bones

in *Elephas maximus* and *Loxodonta africana*. Notations of table 1 are extended by the t-test comparisons of slopes in *n specimens* shown by  $p_{min} < p < p_{max}$  (for details see the electronic supplementary material). Characteristic of a given group of species *forelimb* and *hindlimb bones* are introduced through the fore-bone (humerus, radius, and ulna) and hind-bone (femur and tibia) standard means, respectively. The effective *limb bone* is determined by the overall (5-bone) standard mean. Other notations are the same as in table 1.

The main results obtained by the LS regression in tables 1 and 2 are displayed and analyzed in figure 2.

## Place figure 2

In figure 2, the model predictions for bone slenderness exponent are compared with those of the entire group of proboscideans, Elephantidae, mammals, and modern elephants. As seen from the data presented by the bone-averaged exponents (in table 2) resulting from the LS and RMA species-average statistics (shown by bars), the limb bones of the family Elephantidae are structurally designed likewise those in mammals. The data for extant *Ele-*

*phas maximus* are also quite similar to mammals, whereas the bone exponents in *Loxodonta africana* are distinctly lower (see also figure 1). This implies that the data for *Elephas maximus* as well as the family Elephantidae, are better explained by adaptations to peak muscular forces during locomotion, whereas the limb bones in *Loxodonta africana* are indicative of adaptation to cope with the forces of gravity [2]. The Elephantidae and individual species within this family also have thinner long bones than more primitive proboscideans (Haynes 1991; Christiansen 2007).

### Place figure 3

In figure 3, we examine the allometry exponents of individual bones, with the aim to interpret their adaptation to the patterns of peak elastic forces and stresses. Within the Elephantidae, the similarity in variation of bone slenderness in those three groups is very evident from the parallel lines, as shown in figure 3. When the mechanical origin of the model predictions provided in Methods is taken in consideration, the limb bones in *Elephas maximus* indicate adaptation to complex muscular and, in part, gravity stresses.

It is well established in comparative zoology that the humerus of running parasagittals is loaded differently owing to large muscle attachments and an inclined angle compared to the epipodials, but in elephants the humerus and femur are not very steeply inclined. This is broadly congruent with the observation in figure 3 that the femur, which being almost vertical when the animal stands motionless and much more inclined in running mammals than in fast moving elephants, should involve lower bending and torsional moments in *Elephas maximus* than in other mammals and much less muscular moments in *Loxodonta africana*. Indeed, as predicted by the ESM beyond experimental error, the limb bones in *Loxodonta africana* appear to be adapted for axially compressive stress generated by gravity. Such

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[2] Our sample of *Elephas maximus* has more large juveniles included than in *Loxodonta africana*, and all resulting slopes are generally higher than in *Loxodonta africana* (table 2). Comparing only adult specimens, therefore ignoring ontogenetic adaptations, the radius and femur slopes remain significantly lower in *Loxodonta africana* than *Elephas maximus*, whereas the exponents for humerus, ulna and tibia become non-significantly different (see online supplementary material). In *Loxodonta africana*, all exponents for adult specimens only are similar to the full sample including large juveniles, whereas the slopes in *Elephas maximus* become significantly higher (femur) and lower (tibia). Overall, the LS-average slenderness exponent in adult *Elephas maximus* ( $\lambda_{\text{exp}} = 0.839$ ) remains significantly higher ( $p < 0.05$ ) than in adult *Loxodonta africana* ( $\lambda_{\text{exp}} = 0.662$ ).

a distinction in allometry slopes induced by mechanical adaptation, clearly distinguishes *Loxodonta africana* from *Elephas maximus*, which, in turn appears to bear a mechanical, if not morphological similarity to the limb bones of mammals capable of true running. Accordingly, the limbs of *Elephas maximus* would appear to be more adapted for resisting the forces from limb muscles, which broadly is more consistent with faster forms of locomotion.

As seen in figure 3, the radius and femur in modern elephants expose different loading trends of those in mammals. A consequent distinct mechanical characterization of the hindlimbs and forelimbs is displayed in figure 4.

#### Place figure 4

In figure 4, the differently designed forelimb and hindlimb bones are schematically shown through the hind-fore-limb bone vector, indicating the existence of a gradient in the limb bone functions, likewise gradients in muscle functions in mammals (Biewener et al. 2006) increasing the stability of running (Daley et al. 2007). One can see that the Elephantidae contrasts to mammals in limb bone functions.

## IV. DISCUSSION

### A. Surveying kinematic empirical data

Recent studies have provided new insights and have significantly enhanced our understanding of elephant locomotion. Typically called graviportal, elephants are unable to run with a suspended phase in the stride, and even during fast locomotion, one limb is placed firmly on the ground (Gambaryan 1974). New studies have, however, indicated that fast moving elephants are not merely walking, but that kinetics and kinematics during fast locomotion differ from walking, and numerous locomotor parameters are similar to those of running mammals, for instance offsetting the phase of forelimb and hindlimb footfalls; achieving the transient walk-run duty factors 0.5; and maintenance of pendular locomotor kinematics, typical of walking gaits, for the forelimbs, whereas the hind limbs move with a more spring-like (bouncing) action (Hutchinson et al. 2006; Ren & Hutchinson 2007). Accordingly, at high speeds elephant locomotor kinematics are indicative of walking gaits whereas kinetic analyses indicate running, as in other quadrupedal mammals. The primary

differences are that elephants never achieve a full-body aerial phase during any form of locomotion, although at speeds of just over  $\sim 2 \text{ ms}^{-1}$ , the hind limbs begin exhibiting an aerial phase with bouncing kinetics, implying that the limbs become compliant, whereas the fore-limbs maintain a more straight morphology, consistent with more vaulting mechanical properties (Ren & Hutchinson 2007). Another significant difference from running, quadrupedal mammals, there is no marked change of gait at high speeds, even at Froude numbers  $Fr > 3$ , a value when other quadrupedal animals have changed gaits to a bouncing, running gait with a full-body aerial phase (Alexander 1983, 1989; Alexander & Jayes 1983).

During progressively faster locomotion, elephants initially increase speeds primarily by increments in stride frequency, but at high speeds, further speed increase is facilitated primarily by increments in stride length (Hutchinson et al. 2006). This slow-to-fast gait transition is similar to walking-trotting transition in quadrupedal running mammals, where increments in speed is a function of those in both stride length and frequency, whereas in the case of running gaits with bouncing limb kinetics and a full-body aerial phase is characterized primarily by increments in stride length (e.g., Heglund et al. 1974; Pennycuick 1975, Biewener 1983; Alexander 1983, 1989; Alexander & Jayes 1983). Locomotor kinematic parameters in Asian and African elephants are broadly similar, but statistically significant differences exist, pertaining to relative stride lengths, stride frequencies, stance phase, and duty factor with speed. African elephants have higher duty factors, shorter stride lengths and higher stride frequencies than Asian elephants (Hutchinson et al. 2006). Interestingly, large elephants, such as full grown bulls, appear incapable of reaching the same locomotor intensity as small elephants, and have duty factors  $\beta < 0.5$ , implying that no limb pair ever exhibits an aerial phase; they are, in effect, only walking during fast locomotion. Consequently, this observation may imply that large individuals may exploit the compliance of bone tissue to a lesser extent.

## B. What does the overall-bone statistics tell us?

The theoretical concepts provided in the Methods section permits an interpretation of the limb bone allometric data in terms of the adapted loading patterns. Beyond any modeling, the regression analysis illustrated in figure 1 indicates that the individual limb bones in distinct extant elephants are likely similar in bone ontogeny but they are evidently different

in their mechanical adaptation as revealed by distinct slopes in size proportions. When known theoretical models are employed in terms of the overall-bone slenderness exponent (in figure 2), one can see that the limbs in *Elephas maximus*, as well as in Elephantidae, show a similarity to the limbs of other mammals, broadly exploiting muscular forces during efficient locomotion. This observation agrees with *in vivo* data on the elephant locomotor kinematics having generally many patterns in common with typical tetrapods (e.g., Hutchinson et al. 2006). In contrast, our analysis show that *Loxodonta africana* successfully employs body gravitation and reaction gravitation forces for efficient walking. More specifically, the analysis in figure 2 indicates that the overall-bone averaged slenderness allometry exponent associated with the structure of an effective limb bone (defined in table 2) can be understood in mammals and the Elephantidae (but not intraspecifically in *Loxodonta africana*), by its adaptation to peak muscular forces generated during fast locomotion, whereas the limb bones in *Loxodonta africana* are indicative of adaptation to cope with the forces of gravity more successfully exploiting in walking. This finding also implies that both propodial and epipodial limb bones in mammals are established to be adapted for peak functional bending and torsional stresses (figure 3) by the exploiting of bone compliance, contrasting to more stiffer limbs in Asiatic elephants, as predicted by the ESM (figure 4).

When *Elephas maximus* and *Loxodonta africana* are compared, no contrasting adaptation of any individual limb bone is revealed in figure 3, because all bone lines are parallel. This is not the case of lines lying between mammals as group and elephants. This observation suggests a similarity between bone joint angles generally established for modern elephants during fast locomotion by direct observations, e.g., by Ren et al. (2007). Consequently, bone angles, which are evidently similar in elephants, and distinct from other mammals, indicate differing loading conditions related to limb postures in elephants, extant and extinct, from those of other mammals. More specifically, the epipodial femur, shows in figure 3 its adaptation to complex compression (bending and/or torsion) during bouncing kinematics of the hindlimb involved in fast locomotion, thereby exploiting rather the bone compliance, than the bone stiffness associated with more isometric bone proportion scaling exposing by the forelimb radius, in *Elephas maximus* and forelimb humerus in Elephantidae, thereby contrasting to parasagittal femur and radius. Such mechanical trends are consistent with the kinematic data (Hutchinson et al. 2006) that the hind limbs of modern elephants during fast locomotion are broadly more compliant than the fore limbs. This empirical finding in

modern elephants is now generalized over extinct elephants.

The contrasting postures between mammals as group and elephants can be understood by the different design of fore limbs and hind limbs revealed in figure 4 by the opposed directions of the gradient of the limb functions in locomotor kinematics. As for the small negative gradient in *Loxodonta africana* with respect to *Elephas maximus*, it can be ignored, because the typical statistical error (shown by the bars) exceeds the length of the limb bone vector. In other words, the crossover of the bone lines between the modern elephants can be referred to a small statistical uncertainty that can be ignored, providing a qualitative agreement with the overall similarity in limb postures revealed in figure 3. On the contrary, the observation in figure 4 of the gradient of limb functions for the Elephantidae exceeding the statistical error may suggest a trend for forelimb bones to be more isometric, and also that the forelimb bones in *Elephas maximus* are therefore stiffer than bones in the hind limbs. This also is congruent with the differences in limb locomotor kinematics (Hutchinson et al. 2006), outlined above.

### C. Positive gradient of limb stiffness as major locomotor constraint in elephants

Our study of the allometry of individual limb bones reveals different patterns in limb mechanical adaptation in proboscideans and begs the question how they correlate with kinematic patterns characteristic of modern elephants? Such a correlation is expected, since the mean data on duty factor  $\beta$  in limbs of modern elephants (Hutchinson et al. 2006) are underlaid by the overall-bone (and overall-muscle) limb characterization described here though the limb bone slenderness exponent  $\lambda$ .

Near the walk-run transition in mammals, with the Froude number  $Fr \approx 1$ , the scaling predictions for the forelimb duty factor  $\beta_{FL} = 0.52$  and the hindlimb duty factor  $\beta_{HL} = 0.53$  (estimated on the basis of empirical scaling relations by Alexander & Jayes 1983), provide negative *limb duty factor gradient*  $\Delta\beta$  ( $\equiv \beta_{FL} - \beta_{HL}$ ) for mammals, contrasting with the positive gradient  $\Delta\beta_{ele}$  for elephants (see table 6 in Hutchinson et al. 2006). These data can be related to our LS bone exponent  $\lambda_{FB} = 0.788$  in mammalian forelimb and  $\lambda_{HB} = 0.804$  in mammalian hindlimb, corresponding to the mammalian overall-bone exponent  $\lambda_{exp}^{(mam)} = 0.795$  (table 1) and the negative *limb bone gradient*  $\Delta\lambda_{exp}^{(mam)} = -0.016$  (with,  $\Delta\lambda \equiv \lambda_{FL} - \lambda_{HL}$ ). For elephants, the duty factor gradient  $\Delta\beta > 0$  also correlates to

the bone gradient  $\Delta\lambda > 0$  (figure 4). Indeed, as follows from tables 1 and 2,  $\Delta\lambda_{\text{exp}}^{(ele)} = 0.026$ , for *Elephas maximus*, and  $\Delta\lambda_{ele} = 0.068$ , for Elephantidae. As for the discrepancy in signs between  $\Delta\beta_{\text{exp}}^{(ele)} = 0.026$  (table 4 by Hutchinson et al. 2006) and  $\Delta\lambda_{\text{exp}}^{(ele)} = -0.008$  for the *Loxodonta africana*, it was referred above to the statistical error.

Employing the similarity in limb functions and their gradients observed directly (kinematically) in modern elephants and indirectly (allometrically) via limb bones of extinct and extant elephants, we develop a simple linear model predicting limb duty factors for Elephantidae, which includes more primitive groups of proboscideans (see the electronic supplementary material). The linearization procedure of the mean limb data and their gradients known for living elephants (shown, respectively, by the dashed lines in figure 5 and its inset) results in the duty factor predictions for Elephantidae, as explained in figure 5.

### Place figure 5

The geometrical visualization of locomotory constraints imposed on animal limbs in a certain locomotion mode can be displayed on a  $\lambda$ - $\beta$  diagram presented by figure 5. Such a characterization makes a link between the limb bone and limb bone gradient bone proportions (figure 4) and the limb and limb gradient kinematics (figure 4 by Hutchinson et al. 2006).

The major limb functional difference in mammals as a group and elephants indicated by different orientation of the characteristic vectors shown in figure 5 is due to the difference in signs of the limb stiffness-compliant gradient transferred between fore and hind limbs during the animal's forward propulsion of the body. Running mammals, having hindlimbs which are stiffer than the forelimbs and therefore transfer the positive compliance limb gradient (or negative stiff limb gradient), but they are able to achieve a full-body aerial phase during fast locomotion. In contrast, elephants, transferring negative limb compliance gradient (hindlimb bones are more compliant than forelimb ones) do not achieve a full-body aerial phase during any form of locomotion, though are able to sufficiently reduce the positive stiff limb bone gradient by limb muscles when showing a negative limb duty factor gradient  $\Delta\beta$  during both slow and fast walking gaits (see figure 4B by Hutchinson et al. 2006). However, it is not enough for changing of the positive direction of the limb gradient vector in the  $\lambda$ - $\beta$  diagram, contrasting to mammals (figure 5), since elephants, being naturally constrained

in limb bone proportions, are not able to change sign of the positive gradient in limb bone slenderness  $\Delta\lambda$ . Hence, the preserved excessive positive hindlimb-forelimb stiffness gradient ensured by the corresponding mass-independent and speed-independent positive limb bone slenderness, explains the inability of elephants to perform true running with a full-body aerial phase discussed by Hutchinson et al. 2003. Consequently, in order to move fast they increase stride frequency, mostly exploiting forelimb stiffness, instead of compliance, and in order to increase the stride length, they are forced to use hindlimb bone compliance, instead of stiffness.

#### D. Asian compared with African elephants

Being similar in fast locomotion gaits with respect to the lateral sequence footfall pattern, the Asian, African and most likely extinct elephants (as predicted figure 5) are found to differ in limb bone and perhaps also muscle constraints. All having similar projections of the characteristic vector in the  $\lambda$ - $\beta$  diagram, the limb bone stress indicated by the bone slenderness for the African elephant is significantly distinct from that in other elephants. According to the SSMM, in the Elephantidae and in particular in *Elephas maximus*, the bone off-axial external muscle forces generated during fast locomotion, broadly exceeding body weight and causing a complex bending-torsion elastic bone stress, provide a relatively high level of limb compliance conducted by the structurally adapted limb long bones. In contrast, limb bones in *Loxodonta africana* generally adapted for axial bone compression, are most likely tuned by limb muscles to employ better gravitation reaction forces, in accord with relatively low bone slenderness, explained by the ESM.

Having long bones designed to maintain axial stress and avoiding bending and torsion, African elephants can be expected to exhibit shorter stride lengths and therefore to use higher stride frequencies than Asian elephants, at increased locomotor speeds. From an energetic point of view, this implies the higher energy cost of the Asian elephant locomotion, whereas higher duty factors characteristic of African elephants (figure 5) indicate less bending moments about the joints accommodated ground reaction forces. We infer that Asian elephants, having more compliant limb bones than African elephants, are broadly able to maintain higher speeds more easily that is statistically supported by the observation (via  $\beta < 0.5$ ) of Asian elephants (figure 4A by Hutchinson et al. 2006). Even the the limb duty

factors in Asian and African elephants may achieve those in mammals, the negative gradient for the limb bone compliance limits the maximum stride length and therefore the maximal running speed with respect to mammals.

It is traditionally believed that mechanical differences must be large to produce differences in bone morphology (Frost 1990), but more recent studies have demonstrated that temporal continuous stimulation three orders of magnitude below the maximal peak forces characteristic of fast locomotion (see Rubin & Lanyon 1982) is likely sufficient to produce significant changes in bone morphology (Rubin et al. 2001). African elephants are typically found in open environments and routinely undertake long-distance seasonal migrations at leisurely paces, whereas Asian elephants are mostly found in topologically more heterogeneous, forested environments and appear to undertake fewer and shorter, if any, seasonal migrations (Sikes 1971; McKay 1973; Laws et al. 1975; Sukumar 1991, 1992). Potentially, this could imply subtle differences even in low-force every-day locomotor mechanics imposed by the structure of the environment. Thus, differences in ecology and migratory activity may conceivably be responsible for the subtle differences in locomotor mechanics between African and Asian elephants, as observed by Hutchinson et al. (2006). In this study, more pronounced differences in allometric and mechanical patterns are demonstrated for *Elephas maximus*, which appear more similar to those in other mammals, and *Loxodonta africana*, which is divergent from both and also from the Elephantidae.

On the other hand, neither allometric nor kinematic or kinetic studies deal with forces and bone stresses directly. It remains therefore a challenge to further analyze the reactive-force elastic-stress patterns revealed for limb bones in extant elephants. Nevertheless, there is another difference between the two species of extant elephants congruent with our findings. Because the limb bone pattern for African elephants indicates axial bone stress, not increasing with body mass (Rubin & Lanyon 1982, 1984) and therefore would constitute non-critical stress (Kokshenev 2007), both the mean and maximal body masses for Asian elephants are expected to be below of those for African elephants. Indeed, African elephants appear to be larger on average than Asian elephants; African elephant large bulls routinely weight 5 – 7 tons, whereas 4 – 5 tons is more common for Asian elephant bulls (Wood 1976; Shoshani 1991). Tentative maximal size of African elephant also appears to be distinctly larger. World recorded bulls are as close to or even exceeding 4 m in standing shoulder height, and estimated body masses of 10 – 12 tons (Wood 1976; McFarlan 1992), whereas

Asian elephants are estimated at 3.3 – 3.4 m in shoulder height and around 8 tons (Pilla 1941; Wood 1976; Blashford-Snell & Lenska 1996).

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## Figure Captions

Figure 1. Long bone articular lengths against diaphysial least circumferences in extant elephants. A, humerus; B, ulna; C, femur; D, tibia. Closed squares are *Elephas maximus*; open squares are *Loxodonta africana*. Regression coefficients are shown in table 2.

Figure 2. A comparison of the predictions by the theory of similarity with the bone slenderness exponents observed via the regression slopes in different groups of proboscideans. Notations: open circles are McMahon's predictions for bones adapted for the influence of gravity ( $\lambda_0 = 1, 2/3$ , and  $1/2$  due to GSM, ESM, and SSM); the closed circle shows mean data  $\lambda_{pred} = 0.785$  predicted for the limb bone, which is primarily adapted for resisting peak muscle forces during locomotion [discussed in equation (2) ]. The bars are the mean LS and RMA data for the limb bone characteristic of Proboscidea, Elephantidae, and mammals taken from table 1 and these for *Elephas maximus* and *Loxodonta africana*, taken from table 2. The error bars show statistical variations between the means of regression data.

Figure 3. The observation of trends in limb bone mechanical adaptation in different species. The bars show maximal variations of the mean exponents of individual limb bones. The slenderness exponents in humerus (H), radius (R), ulna (U), femur (F), and tibia (T) are analyzed in view of elastic similarity models. The notations on the symmetry of bone compression follow from the models described in Methods. Other notations correspond to those in figure 2.

Figure 4. Observation of elastic similarity in the effective forelimb bone (humerus, radius, and ulna) and hindlimb bone (femur and tibia). The arrows indicate deviations in the trends of adaptation for forelimb and hindlimb mechanical functions. The bar shows statistical error. Other notations correspond to those in fig. 3.

Figure 5. Limb bone scaling in mammals and elephants against limb kinematics in fast walking. The vector positions and magnitudes indicate the slenderness exponent and duty factor and the vector directions indicate their forelimb-hindlimb gradients. The dashed vector position predicts the limb duty factor  $\beta_{pre} = 0.58$  consistent with  $\lambda_{exp} = 0.790$  for

Elephantidae obtained by liner interpolation between the kinematic data for Asian and African elephants, as shown by the thin dashed line. The corresponding the model duty factor gradient  $\Delta\beta_{mod} = 0.043$  is found in the inset, through the linear extrapolation (shown by the dashed line) of the gradient known for *Elephas maximus* (blue point) and  $\Delta\lambda_{mod} = 0.008$  adopted for the *Loxodonta africana* (green point). Other data are provided above and/or taken from table 4 by Hutchinson et al. 2006.

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